RHOMBOPHOLIS, A PROLACERTIFORM REPTILE FROM THE MIDDLE TRIASSIC OF ENGLAND

by MICHAEL J. BENTON *and* ALICK D. WALKER

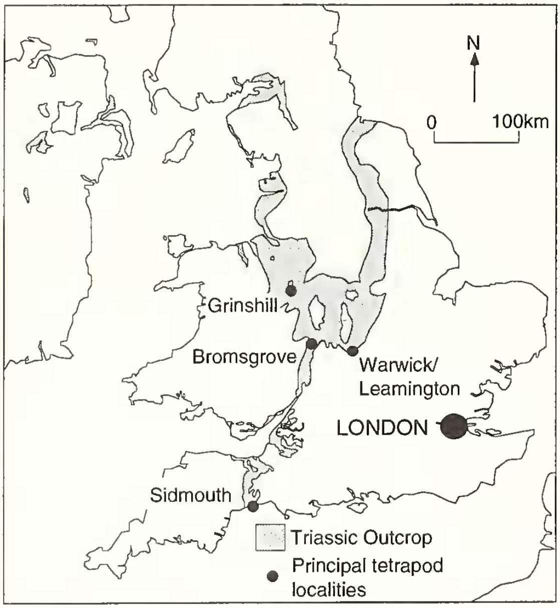
Abstract. The first prolacertiform from the British Isles is described. The type specimen of *Rhombopholis scutulata*, from the Middle Triassic of Warwick, was originally described as a temnospondyl amphibian. The specimen contains bones belonging to a large and a small prolacertiform, both possibly of the same species, as well as scales of a palaeonisciform fish. Prolacertiform characters of the small individual include long and low cervical vertebral neural spines, horizontal neural spine tables on the cervical vertebrae, tall rectangular dorsal vertebral neural spines, and, in a specimen of the presumed larger individual, a strong preacetabular crest on the ilium. Other material of the prolacertiform is noted from Warwick and Bromsgrove. The material is inadequate for confident diagnosis, but it shows closest similarities with *Macrocnemus* from the Middle Triassic of continental Europe.

The Middle Triassic of England has yielded a diverse fauna of fishes, amphibians, and reptiles, together with arthropods and other invertebrates, and plants from a number of localities (Walker 1969; Benton 1990; Milner *et al.* 1990; Benton *et al.* 1994). One of the most prolific units has been the Bromsgrove Sandstone Formation of the Warwick area, and of Bromsgrove, both in the West Midlands of England (Text-fig. 1). The Bromsgrove Sandstone Formation of Warwick has produced a fauna of three amphibian taxa, a stenotosaurine temnospondyl, a cyclotosaurine temnospondyl, and *Mastodonsaurus* (Paton 1974; Milner *et al.* 1990), and two or three reptiles, the rhynchosaur *Rhynchosaurus brodiei* (Benton 1990), the rauisuchian *Bromsgroveia walkeri* (Galton 1985; Benton and Gower in press), and some other possible archosaurs (Walker 1969; Benton and Gower in press). The Bromsgrove Sandstone Formation of Bromsgrove has yielded a similar tetrapod fauna (Walker 1969; Paton 1974), as well as abundant plants (equisetaleans and conifers) and invertebrates and other vertebrates (annelids, bivalves, scorpions, branchiopods, a lungfish, and a perleidid bony fish; Wills 1910). The tetrapod-bearing horizons in both areas have been dated as Anisian (Warrington *in* Benton *et al.* 1994). Fuller details of the faunas may be found in Benton *et al.* (1994) and Benton and Spencer (1995).

One of the most unusual fossils from the Bromsgrove Sandstone Formation, *Rhombopholis scutulata* (Owen, 1842*a*), was interpreted by Owen (1841*a*, 1842*a*, 1842*b*) as a 'labyrinthodont' amphibian, an identification questioned by Miall (1874). Walker (1969) reinterpreted this specimen, and others from Warwick and Bromsgrove, as a prolacertiform reptile possibly related to *Macrocnemus*, a form well known from the Middle Triassic of northern Italy, Switzerland, Germany, and possibly Spain. *Rhombopholis scutulata* (Owen, 1842*a*) is the first-named prolacertiform, pre-dating *Tanystropheus* von Meyer, 1855 and *Protorosaurus* von Meyer, 1856. The purpose of this paper is to describe the English Middle Triassic prolacertiform specimens, including the type material of *Rhombopholis scutulata*, and to reconsider their identifications.

Repository abbreviations. BMNH, The Natural History Museum, London, formerly British Museum (Natural History); CAMSM, Sedgwick Museum, Department of Earth Sciences, Cambridge University; PIMUZ, Paläontologisches Institut und Museum der Universität, Zürich; WARMS, Warwickshire Museum, Warwick.

[Palaeontology, Vol. 39, Part 3, 1996, pp. 763–782, 1 pl.]



TEXT-FIG. 1. The Triassic of England: map showing the distribution of Triassic rocks, and the location of sites mentioned in the text.

MATERIALS

The specimens described here were collected from localities in and around Warwick and at Bromsgrove, the first in 1840. A.D.W. began work on this material in 1967, prepared specimens, and later published a review (Walker 1969). In the present paper, ADW produced Text-figures 4–8 and 10, and Plate 1, and MJB Text-figures 1–3 and 9; the remainder of the work has been carried out jointly. The material comprises:

1. WARMS Gz10, a small block containing 16 major bones (four vertebrae, five limb bones, seven other pieces) and numerous scales. From Leamington Old Quarry (?), collected by Dr G. Lloyd in summer 1840. Described by Owen in February 1841 (Anon. 1841*a*, 1841*b*; Owen 1841*b*, 1842*a*, p. 538, pl. 46, figs 1–5, 1842*b*, pp. 183, 188). Noted by Owen (1860, p. 194, 1866, p. 15), Miall (1874, p. 432), Allen (1909, p. 276), Walker (1969, p. 472), Paton (1974, p. 253), Benton (1990, p. 288), and Benton *et al.* (1994).
2. WARMS Gz21, proximal portion of a left femur. From Coton End Quarry, Warwick, collected by Dr G. Lloyd. Described by Owen (1842*a*, p. 533, pl. 45, figs 11–15, 1842*b*, p. 187) as the proximal end of a humerus of *Labyrinthodon pachygnathus*. Indicated as non-*Labyrinthodon* by Miall (1874, p. 431), and as cf. *Macrocnemus* by Walker (1969, p. 472).
3. WARMS Gz4714, a left ilium. From Coton End Quarry, Warwick, collected by J. W. Kirshaw, and donated in 1872. Noted as cf. *Macrocnemus* by Walker (1969, p. 472).
4. CAMSM G.343, a dorsal vertebra. From the Hilltop Quarries, Bromsgrove, collected by L. J. Wills. Indicated by Wills (1910, p. 264) as a ?rhynchosaur vertebra ('*Hyperodapedon gordoni*'), and reidentified by Walker (1969, p. 472) as cf. *Macrocnemus*.

The elements on WARMS Gz10 appear to comprise fish remains (the scales, and perhaps some bones) and at least two prolacertiform individuals, a small one and a large one, representing either two individuals of a single species, or two species. WARMS Gz21, 4717, and CAMSM G.343 match the large individual of WARMS Gz10 in size.

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA Laurenti, 1768
Subclass DIAPSIDA Osborn, 1903
Infraclass NEODIAPSIDA Benton, 1983*b*
Division ARCHOSAUROMORPHA von Huene, 1946
Order PROLACERTIFORMES Camp, 1945

Genus RHOMBOPHOLIS Owen, 1866

Rhombopholis scutulata (Owen, 1842*a*)

1841*a* *Inisopus* [*sic*] *scutulatus*; Anonymous, p. 2.
1841*b* *Anisopous scutulatus*; Anonymous, p. 4.
1841*a* *Labyrinthodon* [*sic*]; *Owen, pp.* 581, 582.
1842*a* *Labyrinthodon* (*Anisopus*) *scutulatus* Owen, p. 583, pl. 46, figs 1–5.
1842*b* *Labyrinthodon scutulatus* Owen; Owen, pp. 183, 188.
1854 *Labyrinthodon scutulatus* Owen; Morris, p. 350.
1859 *Labyrinthodon scutulatus*; Howell, p. 40.
1860 *Labyrinthodon scutulatus* Owen; Owen, p. 194.
1866 *Rhombopholis scutulata* Owen; Owen, vol. 1, p. 15.
1868 *Labyrinthodon scutulatus* Owen; Hull, pp. 6, 121.
1871 *Labyrinthodon scutulatus* Owen; Phillips, p. 97.
1874 not *Labyrinthodon*; Miall, p. 432.
1890 *Rhombopholis scutulata* Owen; Woodward and Sherborn, p. 207.
1909 *Rhombopholis scutulata* (Owen); Allen, p. 276.
1909 *Labyrinthodon* '*scutulatus*' Owen; Horwood, p. 279.
1969 '*Rhombopholis scutulata*' Owen; Walker, p. 472.
1974 small lepidosaurian reptile; Paton, p. 253.
1990 cf. *Macrocnemus*; Benton, p. 288.

Lectotype. We specify the small reptile on WARMS Gz10 as the lectotype, since it is represented by more elements than the large individual, and these include the diagnostic vertebrae. The slab contains vertebrae, limb bones, and unidentifiable elements of at least two individuals, as well as scales of a palaeonisciform fish, possibly *Gyrolepis*. This is the only specimen described and named by Owen (1842*a*, p. 538; 1842*b*, pp. 183, 188) and the only specimen illustrated in various views by Owen (1842*a*, pl. 46, figs 1–5).

Type locality and horizon. Noted as 'Leamington' by Owen (1841*a*, 1842*a*, 1842*b*), and possibly Old Leamington Quarry (?SP 325666), a source of several finds of fossil tetrapods. An old label reading 'Leamington' is stuck to the side of the block. The source horizon is from about the middle of the Bromsgrove Sandstone Formation, which lies at the top of the Sherwood Sandstone Group, just below its contact with the Mercia Mudstone Group (Warrington *et al.* 1980). The age, obtained by correlation with laterally equivalent units which have been dated by miospores, is Anisian (lower Middle Triassic).

Distribution. Other postulated prolacertiform remains from England, which may or may not pertain to the same taxon as the type specimen of *Rhombopholis scutulata*, include specimens from Coton End Quarry, Warwick (SP 289655) and Hilltop Quarries, Bromsgrove (SO 948698), also from the Bromsgrove Sandstone Formation.

Status of the taxon. It is impossible to give a cladistic diagnosis of the genus *Rhombopholis*, and of the species *R. scutulata*, since the limited material offers no autapomorphies. The taxon is prolacertiform on the basis of the long, low neural spine on the postulated cervical vertebra '1' (Text-fig. 4), a synapomorphy of Prolacertiformes (Benton 1985; Evans 1988), and the ovoid neural spine tables, but there are no features that distinguish this taxon from other prolacertiforms. Further prolacertiform synapomorphies are seen in CAMSM G.343 (the square dorsal neural spine), and in WARMS Gz4714 (the marked preacetabular buttress).

The name *Rhombopholis scutulata* (Owen, 1842*a*) is retained as a metataxon, a taxon that may be distinct from all others, but which currently offers no autapomorphies for its definition (Gauthier 1986).

The type specimen

The lectotype of *Rhombopholis scutulata* (Owen, 1842*a*), WARMS Gz10 (Text-figs 2–3), was collected in the summer of 1840 by Dr G. Lloyd of Leamington, and sent to Richard Owen, who described it in an oral paper to the Geological Society of London on 24 February 1841. In an extended abstract of this paper, Owen (1841*a*, p. 581) stated that 'at Leamington there was discovered a closely and irregularly aggregated group of bones manifestly belonging to the same skeleton, and including four vertebrae more or less complete, portions of ribs, a humerus, a femur, and the two tibiae, one end of a large flat bone, and several small dermal osseous scutae'. He further described (p. 582) the vertebrae as 'batrachian' and commented on the ribs and dermal scutes. No name is given to this form, although the report refers to 'three species of Labyrinthodon [*sic*]', but names only *Labyrinthodon leptognathus* and *L. pachygnathus*. However, the third species was named in newspaper reports (e.g. Anon. 1841*a*, 1841*b*): *Anisopous* was presumably used by Owen in his address, but not reproduced in the long account (Owen 1841*a*). The name *Anisopous* was also used informally by others at this time (e.g. letter from T. Ogier Ward to Owen, dated 26 October [1841], in which he assumes that the small slender *Rhynchosaurus articeps* Owen, 1842*b* from Grinshill, Shropshire is the same animal; Owen Correspondence, Coll. Sherborn, BMNH letter 114).

As a further confusion, Owen (1841*b*, pl. 62A, fig. 3) used the name *Anisodon gracilis* for a specimen from Leamington (?or Warwick) first illustrated by Murchison and Strickland (1840, pl. 29, fig. 9), and interpreted by Owen as an ungual phalanx of *Labyrinthodon* (see also Owen 1842*a*, p. 535). This proved to be part of a premaxilla of *Rhynchosaurus brodiei* Benton, 1990 (see p. 254, fig. 22a). Owen (1842*a*, p. 538, and explanation of pl. 46, figs 1–5) termed the present specimen *Labyrinthodon* (*Anisopus*) *scutulatus*, presumably intending *Anisopus* as a subgeneric name distinguishing this species from the larger forms with sculptured skull bones described earlier in his paper (*L. leptognathus* and *L. pachygnathus*). Owen did not use the name *Anisopus* in a further paper that he must have been writing at about the same time (Owen 1842*b*), the published account of his British Association address given in August 1841, and published in April 1842 (Torrens 1992): the present specimen is named simply *Labyrinthodon scutulatus*.

The name *Anisodon* is a *nomen dubium*, since it was not adequately characterized, and since it is unclear whether it refers to the rhynchosaur alone, or to other material as well, possibly including the present specimen. The name *Anisopus* could stand as valid for the specimen WARMS Gz10, although Owen subsequently abandoned it, perhaps because he found that it was multiply pre-occupied by usages before 1842 for genera of Diptera (Meigen 1803), Crustacea, and Coleoptera. Owen (1860, p. 193) did not use the name *Anisopus*, but repeated (p. 195) his earlier idea that the characters of *L. scutulatus* 'might present differences of subgeneric value' should more remains come to light. In another book, Owen (1866, vol. 1, p. 15) introduced the name *Rhombopholis* as one of two genera of Labyrinthodontia, the other being *Labyrinthodon*. He did not specify that the new name referred to *L. scutulatus*, but its meaning ('rhomboid [scale-] bearer'), and his diagnosis of Labyrinthodontia, including the phrase 'exoskeleton, in some, as small ganoid scales' seems fairly conclusive. One clear feature of WARMS Gz10, referred to by Owen in establishing the species *L. scutulatus* (and the source of its specific name) is the association of the bones with numerous rhomboid 'ganoid' scales, interpreted by Owen as part of the integument of the 'batrachian', and here by us as a chance association with scales of the palaeonisciform fish *Gyrolepis*.

We can find no substantial later reference to *Rhombopholis*, except in reviews of the Bromsgrove Sandstone Formation fauna by Miall (1874), Walker (1969), Paton (1974), Benton (1990), and Benton *et al.* (1994). The genus name is listed by Woodward and Sherborn (1890, p. 207) as an amphibian, and by von Huene (1956, pp. 93–94), Shishkin (1964, pp. 95–96), and Romer (1966, p. 363) as a synonym of *Mastodonsaurus* (of which *Labyrinthodon* is also a synonym), but it is not noted by Carroll (1987).

DESCRIPTION OF WARMS Gz10

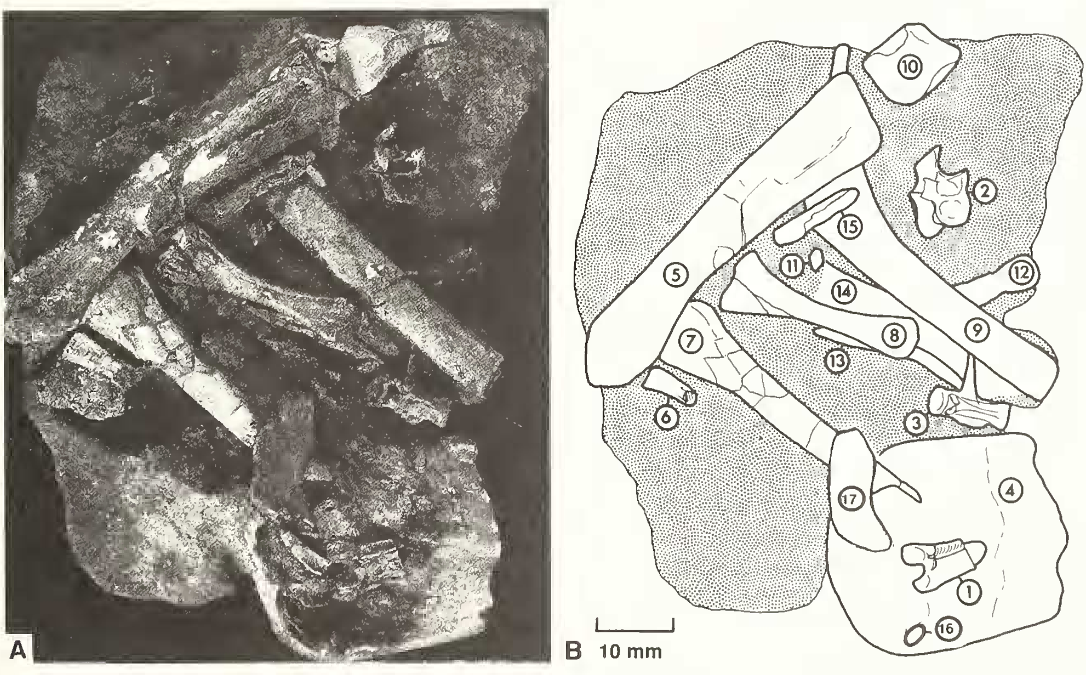
The elements represented in WARMS Gz10 are listed in Table 1, and shown in Text-figures 2–7. The elements numbered 1–3, 6, and possibly 7 and 17, belong to the small animal, elements 4–5, 8–9, and perhaps 10 belong to the large animal, and elements 11 and 16 are fish scales, elements 12–15 possibly fish bones. The material is described in that sequence.

The small animal (Text-figures 2–5)

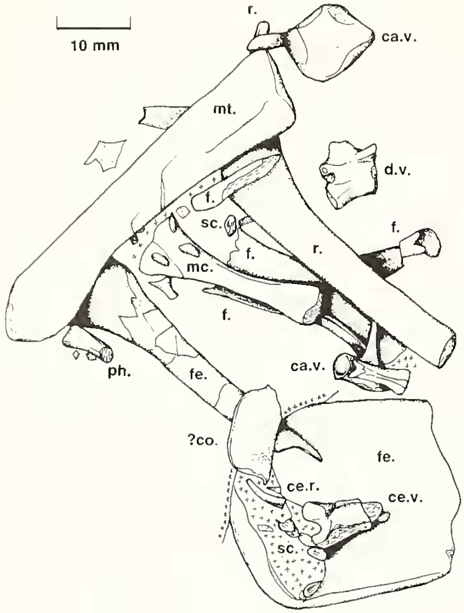
Middle or posterior cervical vertebra. This element ('1', Text-figs 2–4) is broken on the left side and at the back, and the anterior end is a little eroded. The centrum is slightly constricted in the middle, and the ventral margin

TABLE 1. The main elements represented in specimen WARMS Gz10, numbered arbitrarily, and summarizing Owen's (1842*a*, 1842*b*) identification, and the present interpretation. The specimen is illustrated in Text-figures 2–3, and the numbering scheme is reproduced in Text-figure 2B. The identity codes indicate our assignments of elements to the small prolacertiform (S), the large prolacertiform (L), or the fish (F).

Number	Owen's (1842*a*, 1842*b*) identification	Present identification	Identity code
1	vertebra	mid-cervical vertebra	S
2	vertebra	anterior dorsal vertebra	S
3	vertebra	caudal vertebra	S
4	?part of lower jaw	proximal end of right femur	L
5	tibia	metatarsal IV	L
6	?rib	phalanx	S
7	femur	?femur	?S
8	humerus	metacarpal II, III, or IV	L
9	tibia	large rib (passes below 5)	L
10	femur	partial caudal vertebra	?L
11	dermal scute	fish scale	F
12	?vertebra	?fish element	?F
13	?radius/ulna	?fish element	?F
14	?radius/ulna	?fish element	?F
15	?rib	?fish element	?F
16	dermal scute	fish scale	F
17	?	?coracoid	?S



TEXT-FIG. 2. The type specimen of *Rhombopholis scutulata* (WARMS Gz10). A, photograph showing the major elements. B, key to the photograph, showing the major elements and the arbitrary numbering scheme followed in the text.



TEXT-FIG. 3. The type specimen of *Rhombopholis scutulata* (WARMS Gz10). Drawing showing the major elements. Abbreviations: ca.v., caudal vertebra; ce.r., cervical rib; ce.v., cervical vertebra; ?co., possible coracoid; d.v., dorsal vertebra; f., fish bone; fe., femur; mc., metacarpal; mt., metatarsal; ph., phalanx; r., rib; sc., fish scale. Some identifications are tentative (see text).

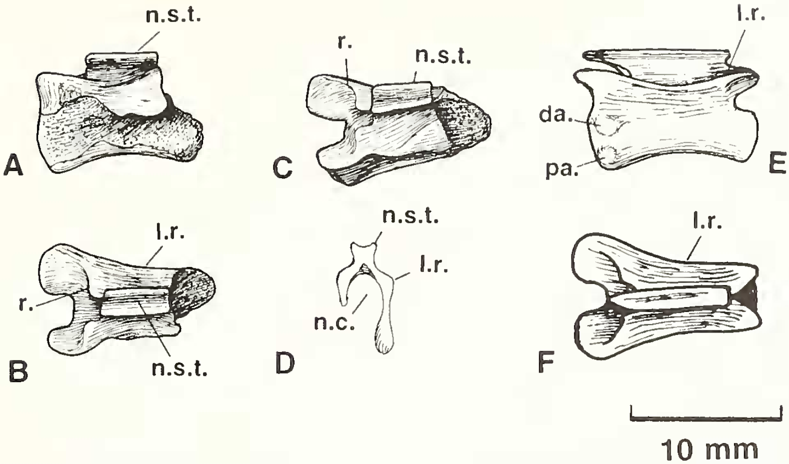
is rounded and without a keel. The right side of the centrum is preserved, but is difficult to observe because it is closely pressed against the large femur head ('4'); there appear to be two rib facets (diapophysis and parapophysis), lying at the anterior margin of the centrum (da., pa., Text-fig. 4E). The prezygapophyseal facets are broad, with a slightly squared outline, and they slope up and laterally at an angle of about 10° above horizontal. The prezygapophyses are linked by a horizontal shelf above the neural canal and in front of the anterior margin of the neural spine. Narrow ridges run from the neural spine to the postero-lateral margin of the prezygapophysis, and from the prezygapophysis to the postzygapophysis (r., l.r., Text-fig. 4B–C, E–F). The postzygapophyses on both sides are incomplete, and lie above a seemingly wide neural canal (n.c., Text-fig. 4D). The neural spine is low and long, and provided with an expanded, horizontal flat top.

This vertebra is similar to posterior cervicals of prolacertiforms, such as *Protorosaurus* (Seeley 1888), *Macrocnemus* (Peyer 1937, p. 98), and *Tanystropheus conspicuus* (von Huene 1908*a*, fig. 243), but not *T. longobardicus* (Wild 1973), because of the great elongation of cervical vertebrae in the last. The closest resemblance of this *Rhombopholis* vertebra is to cervical 6 or 7 of *Prolacerta* (Gow 1975, fig. 21; Colbert 1987, fig. 7), except that the neural spine in the latter is higher. The neural spine table in *Prolacerta* is nearly identical in dorsal view, as it is in *Malerisaurus* (Chatterjee 1980, fig. 8).

Anterior dorsal (? or posterior cervical) vertebra. This vertebra ('2', Text-figs 2–3, 5A–F) has been prepared in the round, and detached from the main block. It is perfectly preserved, except for some damage at the posterior end (Text-fig. 5F). The centrum is constricted in the middle, and passes into the neural arch without an evident suture. The centrum is broader than high, and has a deeply excavated anterior face. The parapophysis is probably represented by a roughened facet half-way down the anterior margin of the centrum (pa., Text-fig. 5D).

The neural canal is ovoid and twice as wide as high (Text-fig. 5A–B). The prezygapophyses are supported on broad pedestals, and diverge widely, sloping up laterally at an angle of about 20° above horizontal. The neural spine is low and capped by a table, as in the cervical vertebra '1'. This neural spine table has a shallow V-shaped cross section and bears a slightly rugose ornament on its upper surface (n.s.t., Text-fig. 5A–C). This table comes to a point, and projects anteriorly over the prezygapophyses. In front of the neural spine, a sharp ridge runs to the prezygapophysis (r., Text-fig. 5A–C). The prezygapophyseal pedestal expands laterally at its base to support the diapophysis (da., Text-fig. 5A–E). The postzygapophyses have facets sloping up laterally at an angle of about 20°, which connect directly to the neural spine table by mediodorsally running ridges on each side.

This specimen resembles the anteriormost dorsals of *Macrocnemus* (Peyer 1937) and *Tanystropheus* (Wild 1973, fig. 52). It resembles the presacral vertebra 10 of *Prolacerta* illustrated by Gow (1975, fig. 21), especially



TEXT-FIG. 4. The type specimen of *Rhombopholis scutulata* (WARMS Gz10). Cervical vertebra, element '1' of the 'small' individual, in: A, left lateral; B, dorsal; C, oblique dorso-lateral; D, posterior; E, restored left lateral; and F, restored dorsal views. Abbreviations: da., diapophysis; l.r., lateral ridge; n.c., neural canal; n.s.t., neural spine table; pa., parapophysis; r., ridge.

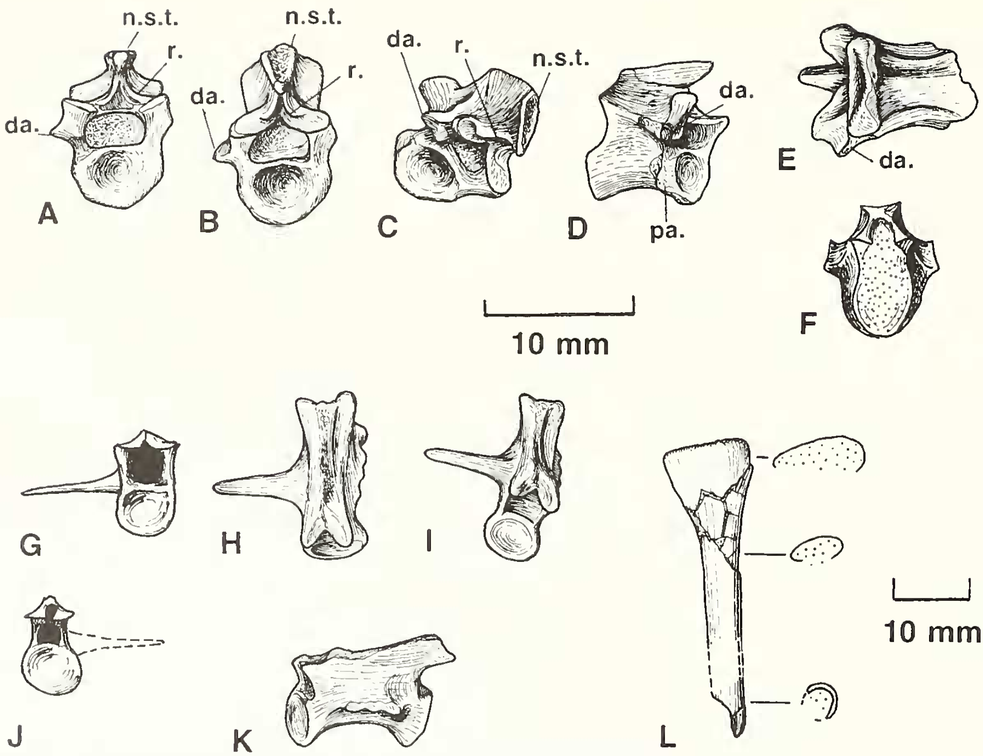
in anterior and posterior views, and also resembles the presacral 7 or 8 of *Malerisaurus* shown by Chatterjee (1980, fig. 8, 1986, fig. 5).

Anterior caudal vertebra. This vertebra ('3', Text-figs 2–3, 5G–K) is nearly complete, lacking only the transverse process on the left side and the neural spine, and having the right side partly obscured by matrix and by element '9'. The centrum is lower and narrower than in the other two vertebrae, and its ventral margin arches up. There is no ventral keel, but there is a bevelled surface for a chevron on the postero-ventral margin. The anterior and posterior faces of the centrum are more circular than those of the other two vertebrae, and they slope back at 10–20° from the vertical.

The neural arch is fused to the centrum without evident suture. The neural canal is bounded by slender vertical walls, and is broader than high in front, but seems more equidimensional behind. The small prezygapophyses slope up laterally at about 20° above horizontal, and they are supported on narrow pedestals on either side of the neural canal. A slender ridge runs back from the lateral margin of the prezygapophysis above the long, slender, horizontal transverse process. The length of the transverse process cannot be estimated since it passes below the large rib '9'. Below the transverse process is a deep longitudinal groove in the side of the centrum (Text-fig. 5K). The postzygapophyses join at the base of the neural spine only a short distance above their articular facets. The apparent great length of the transverse process is not excessive in comparison with *Macrocnemus* (Peyer 1937, pl. 63) and *Tanystropheus antiquus* (Ortlam 1967, pl. 45, fig. 3).

Phalanx. The postulated phalanx ('6', Text-figs 2–3) is a short square-sided element lying close to long bone '5'. It is exposed apparently in ventral view, the uppermost face being flat and depressed below the raised edges. One end is seemingly unbroken and straight and appears to be deeply excavated, probably as a result of erosion of an unfinished cartilaginous portion. The element narrows symmetrically towards the other end, but this is damaged. A distal ligament pit is seen on the side closest to element '7' on the slab.

Femur. Element '7' (Text-figs 2–3, 5L), a possible femur, cannot be identified with certainty. It is a long bone, evidently rather thin-walled and more heavily cracked than all other elements on the slab. If it belonged to the large individual, it would have to be interpreted as a metapodial, but it seems too long and slender to be a metatarsal (cf. '5', Text-figs 2–3) and too long and robust to be a metacarpal (e.g. '8', Text-figs 2–3). The overall shape is like the femur of *Macrocnemus* (e.g. Peyer 1937, figs 27, 36, pls 55, 59–61). The present element is broadest at its (postulated) proximal end, and the expansion is asymmetrical with respect to the shaft. The proximal margin seems to be straight, and the widest expansion is presumably towards the anterior margin, making this a left femur, assuming that the exposed side is dorsal (it is convex up and displays no sign of an internal trochanter nor a concave intertrochanteric fossa). The shaft is relatively straight-sided (Text-fig. 5L),



TEXT-FIG. 5. The type specimen of *Rhombopholis scutulata* (WARMS Gz10). A–F, anterior dorsal, or posterior cervical, vertebra, element '2'; G–K, caudal vertebra, element '3'; and L, femur, element '7'; all from the 'small' individual, in: A, G, anterior; B, I, oblique antero-dorsal; C, oblique right antero-latero-dorsal; D, oblique right antero-lateral; E, ventral; F, J, posterior; H, L, dorsal; and K, left lateral views. Abbreviations: as for Text-figure 4.

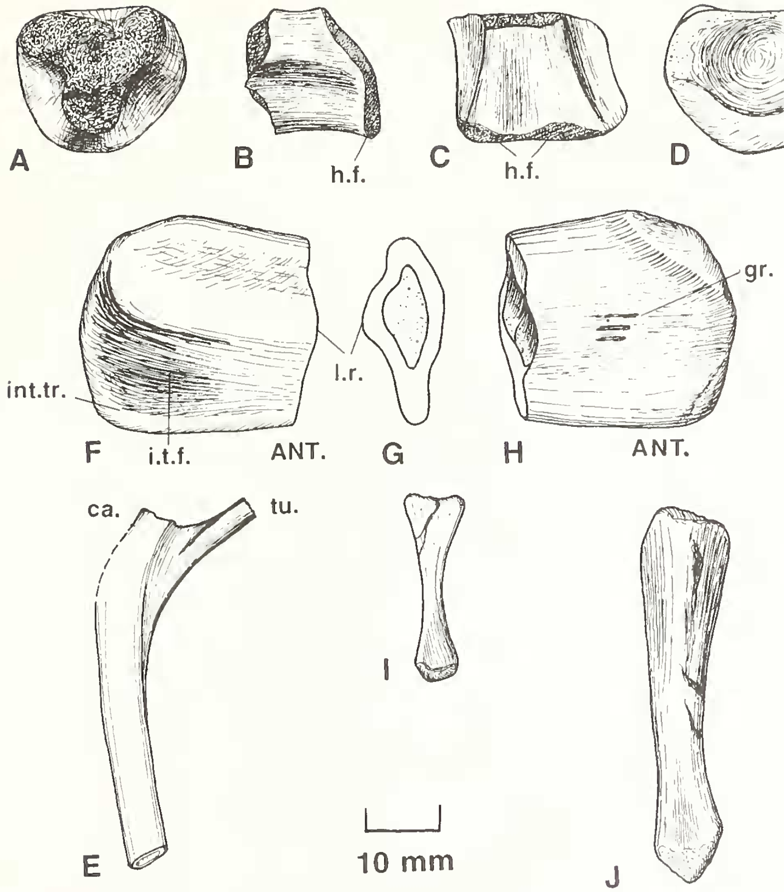
and its cross section changes from being a compressed oval at the proximal end to being more circular distally. The ventral surface of the bone is concealed by matrix, and cannot readily be prepared.

Other elements. Some other bones on the slab may pertain to the small prolacertiform. The thin curved sheet of bone ('17', Text-figs 2–3) located above elements '7' and '4' could be a fragmentary girdle element. Its overall shape and curvature suggest a partial coracoid, by comparison with *Macrocnemus* (Peyer 1937, figs 21–22; Rieppel 1989, figs 2–3). Beside it is an unnumbered thin strap-like element that widens towards one end, where a slight ridge also develops along the outer slightly curved margin. This could be a portion of cervical rib; it is located near the putative cervical vertebra '1'.

The large animal (Text-figs 2–3, 6)

Partial caudal vertebra. Partial vertebra '10' (Text-figs 2–3, 6A–D) is the posterior end of a centrum. The cross section is trefoil-shaped, the ventral margin of the centrum being rounded, and the sides expanding above a shallow groove on each side. Towards the posterior margin, the ventral surface expands, and is marked by a shallow midline groove behind two facets, presumably for a Y-shaped chevron (h.f., Text-fig. 6B–C). The posterior articular face of the centrum is subcircular in shape and slightly concave. If the vertebra were in proportion to the small caudal ('3', Text-figs 2–3, 5G–K), the preserved portion would represent only the posterior one-third or one-quarter of the centrum.

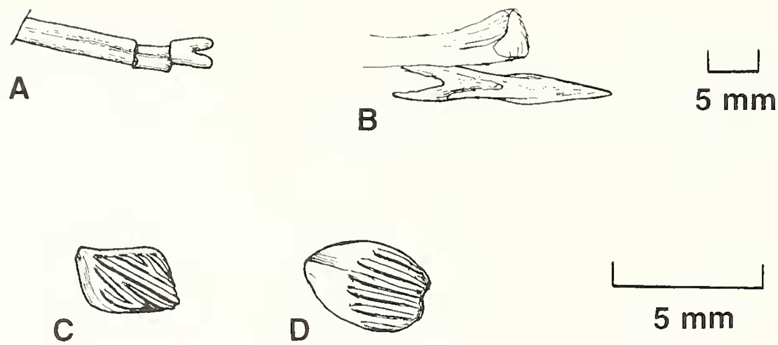
Rib. Element '9' (Text-figs 2–3, 6E) was not clearly identifiable until ADW prepared the specimen, and the proximal end was found to pass under element '5', and to branch. The shaft is nearly straight, and flattened



TEXT-FIG. 6. The type specimen of *Rhombopholis scutulata* (WARMS Gz10). A–D, partial caudal centrum, element '10'; E, rib, element '9'; F–H, proximal end of the right femur, element '4'; I, metacarpal, element '8'; and J, metatarsal, element '5', all of the 'large' individual, in: A, anterior; B, left lateral; C, F, I, ventral; D, posterior; G, cross sectional; and, H, J, dorsal views. Abbreviations: ANT, anterior; ca., capitulum; h.f., haemapophyseal facet; i.t.f., intertrochanteric fossa; int.tr., internal trochanter; l.r., lateral ridge; tu., tuberculum.

in cross section. The proximal head expands widely, and splits into capitulum and tuberculum (ca., tu., Text-fig. 6E). Both processes are broken and appear to be hollow, the capitulum being broad and bordering a depressed area that joins on to the smaller tuberculum, which is cylindrical in shape. The rib is presumably from the anterior thoracic region: it is too broad to be a typical cervical rib, and is double-headed. It is comparable to an anterior thoracic rib of *Macrocnemus* (Peyer 1937, p. 43, pl. 62, fig. 2a) or *Tanystropheus* (Wild 1973, fig. 35): mid- and posterior thoracic ribs are single-headed in these taxa.

Right femur. The proximal end of a large right femur ('4', Text-figs 2–3, 6F–H) was identified by Owen (1842*a*, p. 539) as possibly part of a large jaw bone, but further preparation of the back of the specimen by ADW has confirmed its true identity. The specimen is somewhat crushed. The proximal face is roughened, having possibly been cartilaginous and incompletely preserved. The lateral ridge (l.r., Text-fig. 6F–G) lies closer to the posterior margin of the element, and the bone surface passes into a slight convexity towards that margin. On the anterior side of the lateral ridge, the surface of the bone is more concave, and is rather deeply excavated towards the proximal margin, presumably forming the intertrochanteric fossa (i.t.f., Text-fig. 6F). This deep concavity becomes shallower and less pronounced distally.



TEXT-FIG. 7. The type specimen of *Rhombopholis scutulata* (WARMS Gz10). Postulated fish remains, probably palaeonisciform, possibly from *Gyrolepis*. A–B, isolated fish elements, possibly midline scales, elements 12 and 13; C–D, two scales, elements 11 and 16.

On the dorsal side of the bone (Text-fig. 6H), the surface is rather flat towards the anterior margin, but convex posteriorly. Near the proximal end are two broad roughened facets, the anterior of which may be an internal trochanter (int.tr., Text-fig. 6F). In the middle of the shaft are three or four deep longitudinal grooves (gr., Text-fig. 6H) that pass into the bone distally, possibly associated with the insertion of the puboischiofemoralis internus muscle.

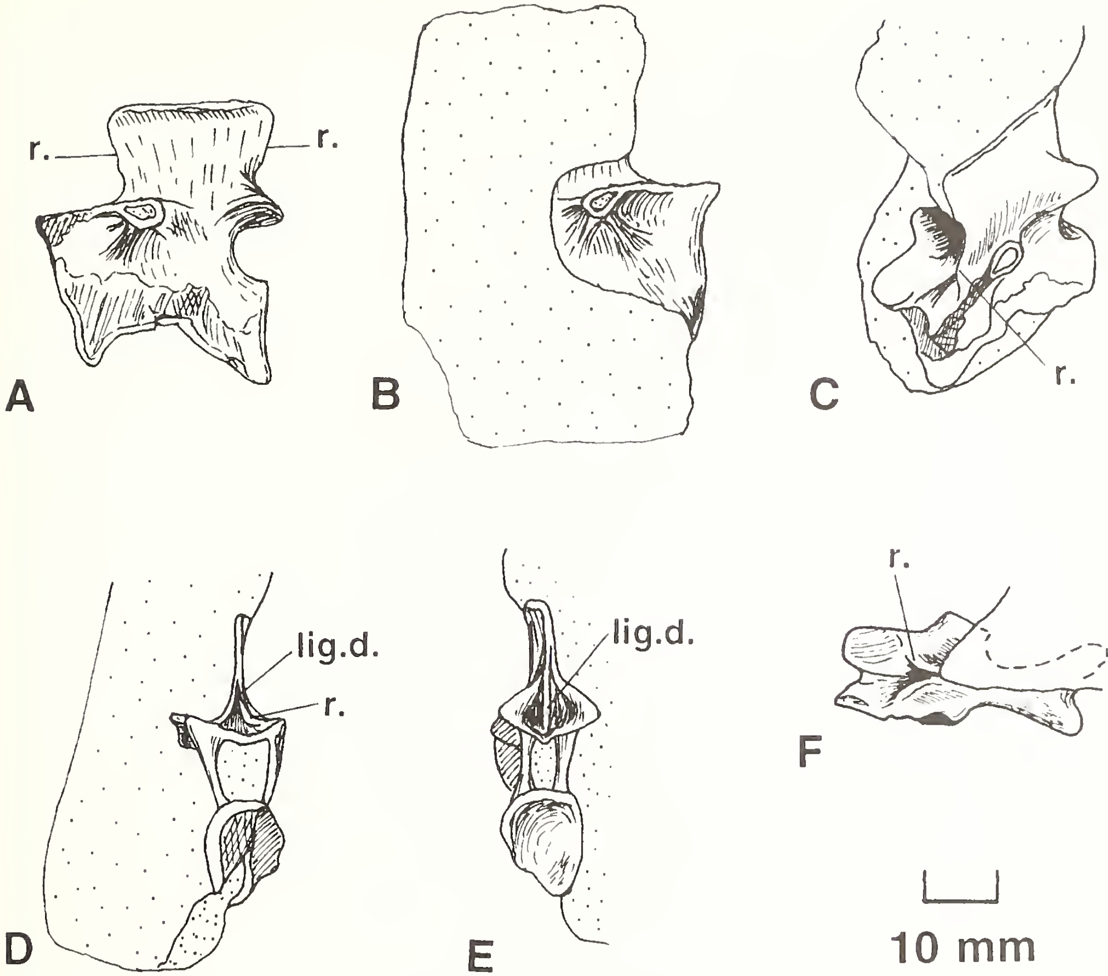
In overall shape, the proximal head of this femur is nearly indistinguishable from those of *Malerisaurus* (Chatterjee 1980, fig. 10, 1986, fig. 7), *Tanystropheus conspicuus* (von Huene 1932, fig. 3) and *T. longobardicus* (Wild 1973, fig. 73). The 'Cava Tre Fontane 1936' specimen of *Macrocnemus* (PIMUZ T2477) shows a near-identical slightly crushed right femur head, bearing also three or four grooves on the dorsal side, as in the present specimen (ADW, pers. obs.; pl. 1, fig. 2).

Metatarsal (?) A presumed metatarsal ('5', Text-figs 2–3, 6J), identified by Owen (1842*a*, p. 539) as a femur, matches the proximal femur end in size. This element cannot be a femur, or other major long bone, of the small animal since it is nearly symmetrical on the visible face. At the presumed proximal end, the element rises to a midline ridge on top, but is either flat, or slightly concave, below. The shaft in its middle portion is flat in cross section, and becomes only a little thicker towards the distal end. Distally, the shaft widens a little and a shallow midline concavity appears on the top surface. The articular facets at the distal end are rugose and unfinished, and the lateral angles may be missing. The whole element curves gently to the right, as viewed, and, if this edge is seen in dorsal view, this bone would be a left metatarsal. The proportions of the bone, and the markedly triangular proximal end, suggest that this is metatarsal IV, by comparison with the foot of *Macrocnemus* (Peyer 1937, pl. 55; Rieppel 1989).

Metacarpal (?) A postulated metacarpal ('8', Text-figs 2–3, 6I) is a smaller element. The exposed surface is relatively flat, and rather broader proximally than distally. The distal end is twisted 10–15° medially with respect to the rest of the bone. The distal articular facets are rugose and incomplete. If the element is viewed from its ventral surface, it is assumed to come from the left manus because the distal end twists slightly medially. In comparison with the manus of *Macrocnemus* (Peyer 1937, p. 66; Rieppel 1989, fig. 5), the proportions of length:maximum width, about 4:1, match metacarpals II or III best.

Palaeonisciform fish (Text-figs 2–3, 7)

The remaining elements may be fish bones ('12'–'15') and scales ('11', '16', and unnumbered). Element '12' (Text-figs 2–3, 8A) may be the 'fourth vertebra' referred to by Owen (1842*a*). It extends a long way beneath the rib '9', and its end could not be exposed during preparation by ADW; hence it cannot be a vertebra. It is a bilaterally symmetrical slender bone with a midline groove, and is rather damaged. It resembles, in its slenderness and mode of preservation, element '13' (Text-figs 2–3, 8B) which is also bilaterally symmetrical. Bone '13' appears to run to a point at one end, partly concealed by a scale below vertebra '3', and it bears a shallow groove along the midline, which deepens with a clear step about half-way along. The other end of bone '13', partly beneath the metacarpal '8', is divided into two narrow processes separated by a deep V-

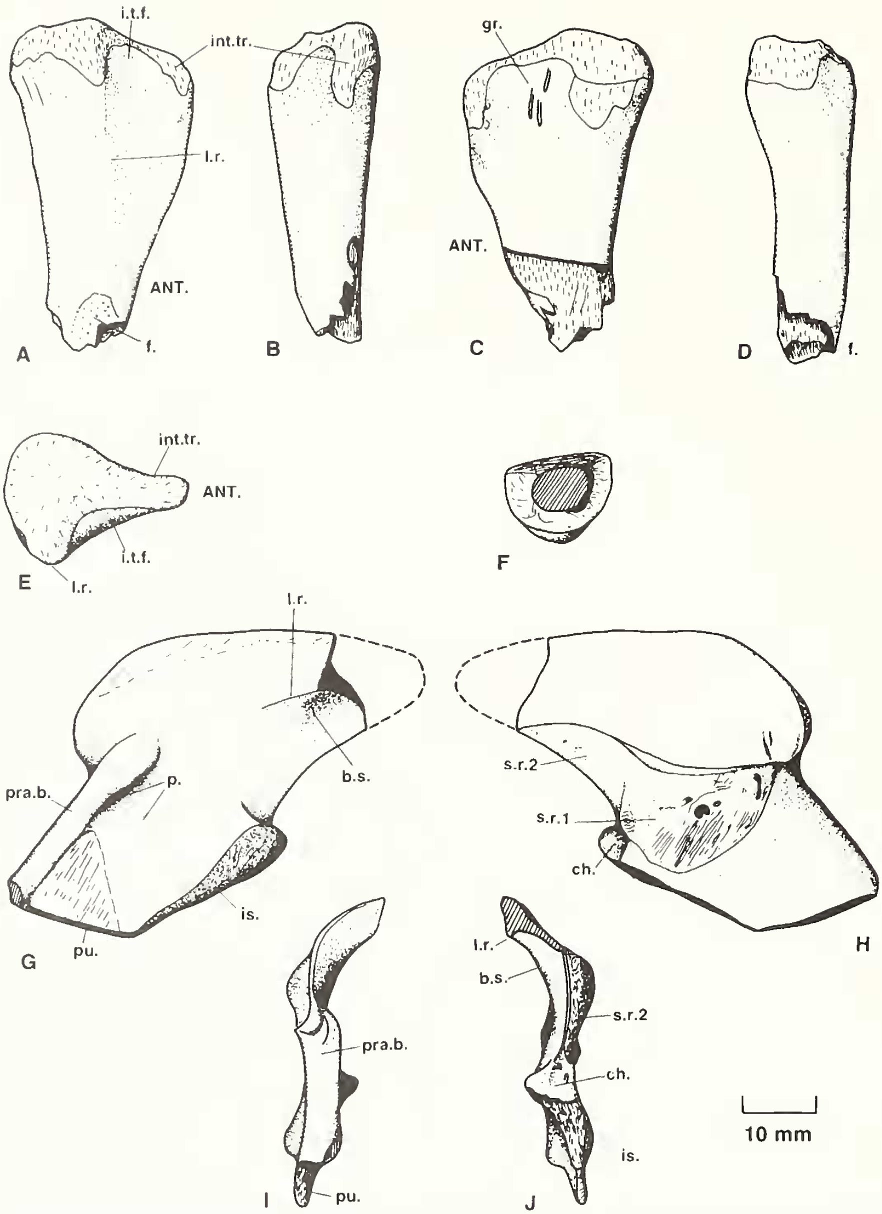


TEXT-FIG. 8. Dorsal vertebra of a prolacertiform, possibly *Rhombopholis* (CAMSM G.343), in: A, left lateral; B, right lateral; C, oblique left latero-dorsal; D, anterior; E, posterior; and F, dorsal views. The specimen is still partly enclosed in sandstone (broad stipple). Abbreviations: lig.d., insertion for ligamentum dorsale; r., ridge.

shaped notch. Elements '14' and '15' (Text-figs 2–3) may also be fish bones. The first is a straight flat element, slightly convex as viewed, and with a longitudinally striated surface. Element '15' is narrower, but also straight, and bearing a similar surface sculpture. It is broken, and its original size and shape cannot be determined. Owen (1842*a*, p. 539) referred to elements '13' and '14' as showing '... nearest resemblance to the anchylosed radius and ulna of the Frog'.

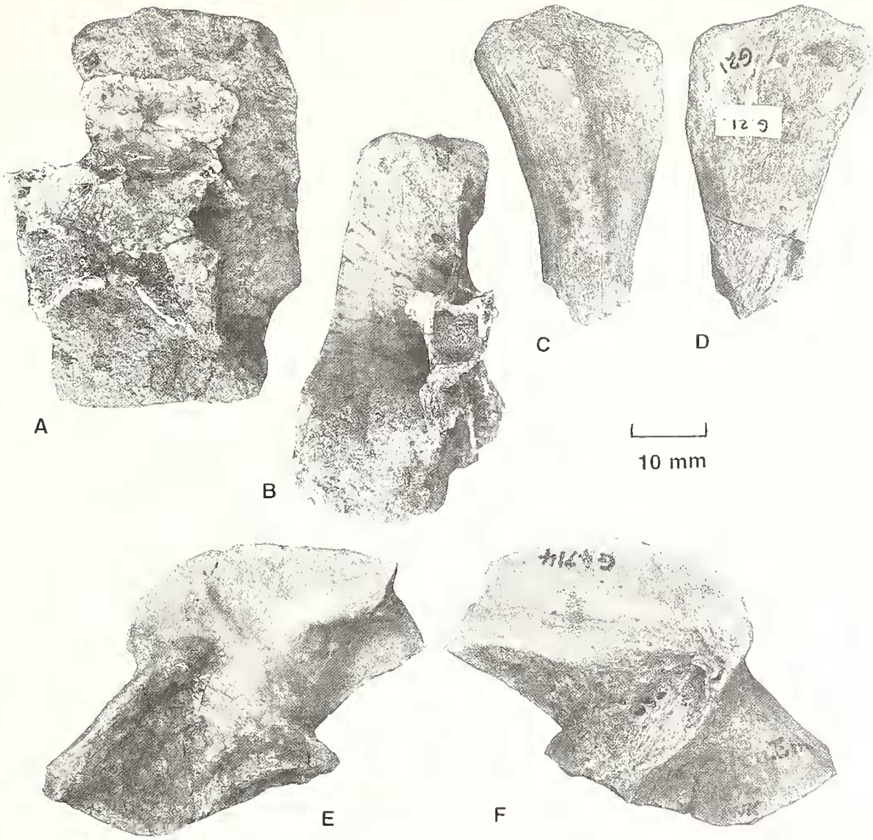
The fish scales, elements '11' and '16', as well as 13 other unnumbered examples (Text-figs 2–3) were identified by Owen (1842*a*, pp. 538, 540, pl. 46, fig. 5) as dermal scutes belonging, with the other bones, to the amphibian *Labyrinthodon*. The scale '11' (Text-fig. 7C) is rhomboid in shape, with rounded angles, and it bears a deeply incised sculpture of branching ridges, seven in all, running subparallel to the long axis, and extending into a slightly dentate posterior margin. The anterior margin is smooth, presumably where it was overlapped by adjoining scales. Scale '16' (Text-fig. 7D) is more ovoid, and the six longitudinal ridges do not branch. The anterior area of underlap is larger than in the preceding scale. In both cases, the ridged part of the scale is elevated above the level of the smooth area.

The identity of the fish bones and scales is difficult to determine. Element '13' (Text-fig. 7B) could be a midline fulcral scale from the dorsal or caudal fin, based on the observation of its symmetry, its thinness, and



TEXT-FIG. 9. Specimens of a prolacertiform, possibly *Rhombopholis*. A–F, proximal end of a left femur (WARMS Gz21), and G–J, left ilium (WARMS Gz4714), in: A, ventral; B, I, anterior; C, dorsal; D, J, posterior; E, proximal; F, distal; G, lateral; and, H, medial views. Abbreviations: ANT., anterior; b.s., brevis shelf; ch., channel; f., facet for muscle; gr., groove; i.t.f., intertrochanteric fossa; int.tr., internal trochanter; is., ischiadic facet; l.r., lateral ridge; p., pits; pu., pubic facet; pra.b., preacetabular buttress; s.r.l.; s.r.2., attachment sites for sacral ribs 1 and 2.

the potential for the pointed end of an identical element to fit into the recessed V-shaped end. Element '12', also symmetrical and with a V-shaped end, could be some other midline scale. The other bones could be skull elements. The scales come from different parts of the body, the ovoid one ('16') possibly from the base of a fin or the tail.



TEXT-FIG. 10. Specimens of a prolacertiform, possibly *Rhombopholis*. A–B, dorsal vertebra (CAMSM G.343), partly enclosed in sandstone, in: A, left lateral; B, anterior views. C–D, proximal end of a left femur (WARMS Gz21), in: C, ventral and D, dorsal views. E–F, left ilium (WARMS Gz4714), in: E, lateral and, F, medial views.

Comparison with common Middle Triassic fishes suggests that the bones and scales here may come from a paleonisciform bony fish such as *Gyrolepis*. The scales are very like those of typical *G. albertii* Agassiz, 1833, or some related species, common in the Muschelkalk of Germany (e.g. Oertle 1928, pp. 357–369, pls 31–32; Schmidt 1928, pp. 356–357). The genus *Gyrolepis* is known principally from the Middle Triassic of central Europe, but also from the Lower Triassic of eastern Asia, the Middle Triassic of South America, and the Upper Triassic of Europe and North America. The scales do not pertain to the perleidid *Dipteronotus* from the Bromsgrove Sandstone Formation and the Otter Sandstone Formation (Gardiner *in* Milner *et al.* 1990), the only other actinopterygian from rocks of this age in England. *Gyrolepis* has hitherto been recorded in England from the Upper Triassic Dane Hills Sandstone Member of Leicester (Horwood 1908; von Huene 1908*b*), from the Blue Anchor Formation (Tea Green Marl) of various localities (Warrington 1976), and from the Westbury Formation everywhere (Storrs 1994).

Other material of a 'large' prolacertiform (Text-figures 8–10)

Three other bones from the Bromsgrove Sandstone Formation may belong to the large prolacertiform, a dorsal vertebra (CAMSM G.343), the proximal end of a left femur (WARMS Gz21), and possibly a left ilium (WARMS Gz4714).

Dorsal vertebra. Vertebra CAMSM G.343 (Text-figs 8, 10A–B) is slightly crushed, and lacks the left surface of the centrum. It has been prepared to show the left side and part of the right-hand side. The centrum is deeply constricted ventrally and laterally, and its articular ends are set at a slope of about 20° from the vertical. The anterior articular face of the centrum is broken away, and the posterior face is largely filled with sediment, but it is deeply concave, and ovoid in shape. There is no parapophysis.

There is no evident suture between the centrum and neural arch. The neural canal is nearly square in anterior view, and is narrower in posterior view. The prezygapophyses bear broad circular articular facets, oriented outwards at an angle of 10° or less above horizontal. Two ridges (r., Text-fig. 8C–D, F) run from the anterior margin of the neural spine to the prezygapophyses. The prezygapophyseal shelf extends back to form the anterior margin of the transverse process, which is directed a little upwards. Neither transverse process is complete, but the right-hand one (Text-figs 8B–D, F, 10B) shows most detail. The process is a thin lamina anteriorly that thickens backwards above three radiating narrow buttresses (Text-fig. 8B), strikingly similar to those in a mid-dorsal vertebra of *Tanystropheus* (Wild 1973, fig. 54).

The postzygapophyses (Text-figs 8A, C, E–F, 10A) bear broad subcircular articular facets oriented at a low angle above horizontal. The postzygapophyseal pedestals run high up the posterior margin of the neural spine. The neural spine is a tall subquadratic thin sheet of bone with a near-vertical anterior margin (Text-figs 8A, 10A), which splits into two sharp ridges, on either side of a deep cleft for the ligamentum dorsale (lig.d., Text-fig. 8D). The top of the neural spine is nearly at right angles to the anterior margin, and there is only a slight expansion. There appears to be a narrow midline lamina of bone on the posterior margin of the spine, presumably the site of insertion of the ligamentum dorsale (lig.d., Text-fig. 8E).

This vertebra is presumably a middle to posterior dorsal, since it lacks a parapophysis (present in cervicals and anterior dorsals of *Macrocnemus* and *Tanystropheus*; Peyer 1937; Wild 1973). The overall shape, with a high neural spine, indicates a vertebra from the lumbar region, by comparison with *Macrocnemus* and *Tanystropheus* (Wild 1973, fig. 54). The vertebra shows two characters noted by Peyer (1937, p. 19) as typical of *Macrocnemus*: the neural spines are long and adjacent ones would touch when the vertebrae are articulated. The latter feature is seen also in *Prolacerta* (Colbert 1987, p. 11) and *Malerisaurus* (Chatterjee 1980, p. 17), but these taxa seem to have rather shorter neural spines, although Gow (1975) noted that neural spine length alternates between short and long in the dorsal vertebral column of *Prolacerta*. 'The 'Cava Tre Fontane 1936' specimen of *Macrocnemus* (PIMUZ T2477) shows a longitudinal ridge or lamella between the prezygapophysis and the transverse process in three mid-dorsal vertebrae, although their transverse processes seem to be wider (ADW, pers. obs.; Pl. 1, fig. 2).

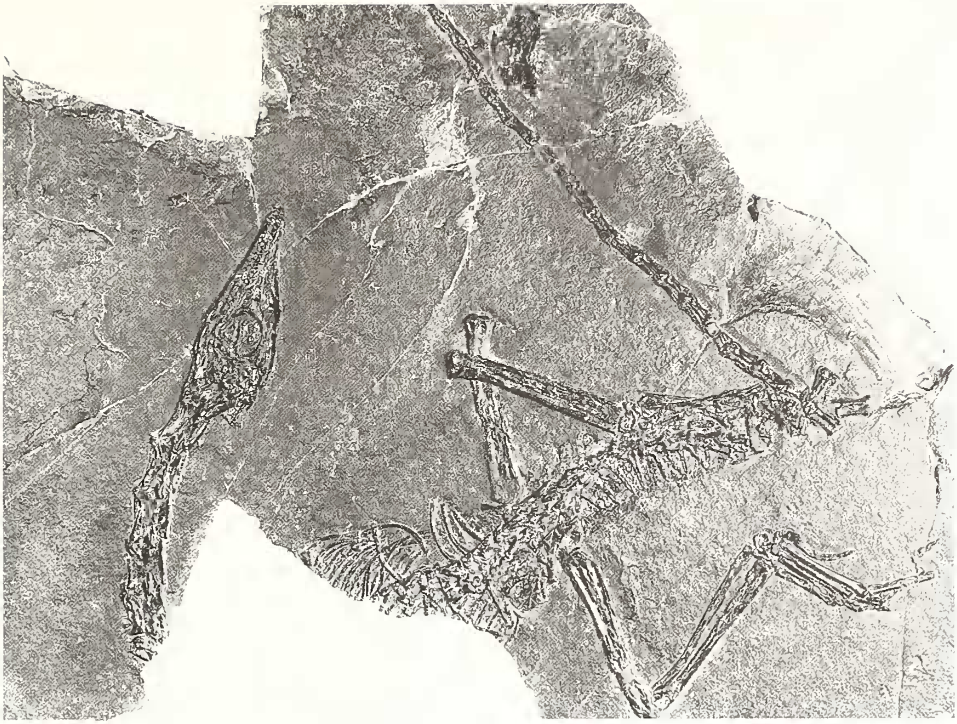
Left femur. The proximal end of a left femur (WARMS Gz21) is similar in size to the large proximal femur end '4' in WARMS Gz10, but rather more of the specimen is preserved, extending to the shaft. The specimen is virtually uncrushed, but is rather eroded. The expanded proximal end bears a substantial lateral ridge (l.r., Text-fig. 9A, E), running close to the posterior side. The heavily abraded proximal articular surface consists of a major ovoid head on the posterior side and a lower narrower anterior expansion terminating in the internal trochanter (int.tr., Text-fig. 9A–B, E). There is a deep intertrochanteric fossa (i.t.f., Text-fig. 9A, E) near the proximal end. Near the distal margin, the ventral ridge dips into the beginning of a rugose flat facet, possibly part of a muscle insertion site (f., Text-fig. 9A, D).

The dorsal face of the bone (Text-figs 9C, 10D) is rather flatter than the ventral, showing a slight convexity distal to the main articular head, and a slight concavity anteriorly. There are also three or four sharp-sided grooves deepening into the bone distally in this area (gr., Text-fig. 9C), as in WARMS Gz10 (cf. Text-fig. 6H). These grooves lie in a slightly concave area, presumably representing the insertion point of the puboischiofemoralis internus muscle. The shaft is slender and subtriangular in section distally (Text-fig. 9F), and contains a subcircular sediment-filled cavity.

EXPLANATION OF PLATE 1

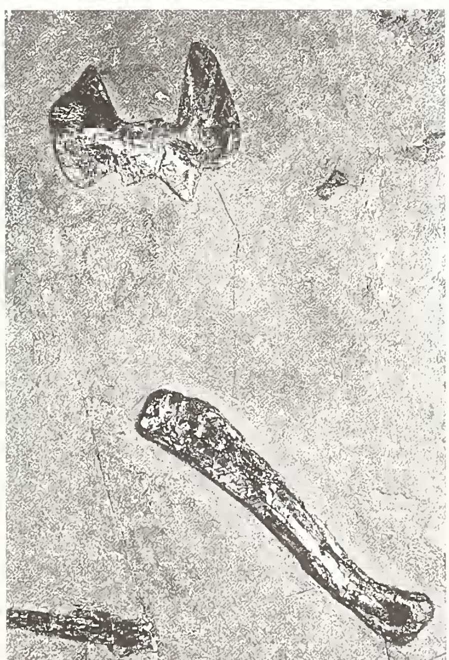
Figs 1–3. Specimens of *Macrocnemus bassanii* (von Nopcsa, 1931). 1, the 'Alla Cascina, 1933' specimen (PIMUZ A III/208), showing a good head and neck, a partial posterior trunk, hindlimbs, and tail; ×0·7. 2, the 'Cava Tre Fontane, 1936' specimen (PIMUZ T2477), showing a skull, partial hindlimb and pelvic girdle, and anterior tail; the right femur lies at top left just beside the back of the skull; the left ilium lies just left of the snout tip, and the left femur and lower limb just below; the anterior caudals are seen in ventral view in the bottom left-hand; ×0·85. 3, the 'Point 902, 1960' specimen (PIMUZ T2470), a detail showing the left ilium and ischium in contact, viewed medially (ilium to the right) and the left femur viewed laterally; ×0·5.

PLATE 1



1

2



3

BENTON and WALKER, *Macrocnemus*

The original lengths of the two large proximal femoral fragments, in WARMS Gz10 and Gz21, may be estimated by comparison with *Macrocnemus*. In the least crushed example, 'Besano II' (PIMUZ T2476), the femur is 72 mm long and 15 mm wide, a ratio of proximal breadth: length of 4·8. Scaling with this factor, the large femur in WARMS Gz10 would have been approximately 144 mm long, and femur WARMS Gz21 would have been 134 mm long.

Left ilium. The left ilium (WARMS Gz4714) is nearly complete, missing only the tip of its posterior dorsal process, and being abraded a little at the anterior end of the iliac blade, and along the pubic and ischiadic facets (Text-figs 9G–H, 10E–F). The dorsal blade has a short anterior process and a longer posterior one. The dorsal margin is thin, curves gently posterolaterally when viewed from above, and the blade is nearly vertical in its anterodorsal portion. There is a slightly roughened area along the anterior portion of the dorsal edge of the iliac blade, probably for the origin of the iliotibialis muscle. A marked ridge rises on the lateral face (l.r., Text-fig. 9G) and extends towards the missing posterior tip. The ridge is roughly triangular in section, and marks the upper margin of a deeply excavated recess, the brevis shelf (b.s., Text-fig. 9G, J), the probable site of origin of the iliofibularis and caudifemoralis brevis muscles. At this point, the iliac blade bends sharply down to a narrow ventral margin. A channel runs from below the lateral ridge, round the posterior margin of the iliac neck, and below the sacral rib attachments where the surface is rugose (ch., Text-fig. 9H, J).

The acetabular region of the ilium is broad (Text-figs 9G, 10E). The anterior edge is greatly thickened as a strong column of bone, a preacetabular buttress, that starts high on the blade as a rounded projection (pra.b., Text-fig. 9G, I). Behind this, the acetabulum is shallow and bears two deep pits (original or damage?) at the top (p., Text-fig. 9G), and a roughened area below which may mark an area of cartilage. The posterior margin of the acetabulum is also thickened. The ventral articular surfaces for the pubis and ischium are clearly set off (pu., is., Text-fig. 9G): the latter is more massive. The preacetabular buttress and the posteroventral region of the acetabulum bear a rugose ornament.

In medial view (Text-figs 9H, 10F), the ilium is divided into three areas. The dorsal part of the blade is smooth, and curves up and laterally to the thin dorsal edge. Beneath this is a rugose and pitted triangular area, bearing two facets, a large subcircular one for the distal end of sacral rib 1, and a smaller triangular one for sacral rib 2 (s.r.1, s.r.2, Text-fig. 9H). The latter facet is set at a sharp angle to the former. Below these facets, a convex surface forms the medial wall of the acetabulum, and curves round to join the preacetabular buttress.

Relatively few prolacertiform ilia have been illustrated with sufficient clarity for comparisons to be made. The ilium of *Prolacerta* (Gow 1975, fig. 24A) seems strikingly similar, having a heavy preacetabular buttress, a long posterior iliac blade, a short anterior process, and a marked lateral ridge. *Malerisaurus* also has a marked lateral ridge, and the outline shape of the ilium (Chatterjee 1980, fig. 10a) is similar to WARMS Gz4714, as is that of *Tanystropheus* (Wild 1973, fig. 71). The 'Point 902 1960' specimen of *Macrocnemus* (PIMUZ T2470) shows an excellent left ilium (Pl. 1, fig. 3) which is like WARMS Gz4714, although it is about half the size (ADW, pers. obs.).

COMPARISONS

The specimens described here could belong to a variety of animals. There are five sets of materials to be assessed, assuming that the specimens assigned to the 'small individual' and the 'large individual' on WARMS Gz10 have been correctly associated. These five sets are the two groupings on WARMS Gz10, the dorsal vertebra (CAMSM G.343), the left ilium (WARMS Gz4714), and the partial left femur (WARMS Gz21). The tetrapods that may be considered include temnospondyl amphibians, procolophonids, rhynchosaurs, trilophosaurs, prolacertiforms, archosaurs, and synapsids, all typical of Middle Triassic terrestrial faunas (e.g. Benton 1983*a*; Benton *et al.* 1994).

Temnospondyls and procolophonids may be ruled out, since all elements – vertebrae, limb girdle bones, and limb bones – are quite different in appearance. Likewise, the vertebrae and limb elements cannot be matched with any Triassic synapsid taxon (cf. Kemp 1982). As for archosaurs, most Middle Triassic groups (e.g. Erythrosuchidae, Ctenosauriscidae, Proterochampsidae, Rauisuchidae, Poposauridae) were much larger than these elements, and none of the bones corresponds (cf. Charig *et al.* 1976). The dorsal vertebra (CAMSM G.343) could be interpreted as archosaurian, but the neural spine and centrum are much longer anteroposteriorly than in corresponding dorsals of a variety of Triassic archosaurs (Charig *et al.* 1976, pp. 49, 50, 104). The ilium and the femora cannot be matched with any known archosaur, and indeed there is no sign of a fourth trochanter, an archosaur synapomorphy, in the present material. The groups remaining for consideration are the rhynchosaurs, trilophosaurs, and prolacertiforms.

None of the bones can be compared to those of rhynchosaurs, whether small or large ones (von Huene 1938; Benton 1983*b*, 1990). Rhynchosaurs have short neural spines on their cervical and dorsal vertebrae, and the cervicals are not elongate. The ilium of *Rhombopholis* is most like that of the much larger *Stenaulorhynchus* (von Huene 1938), but the rhynchosaurs have a more symmetrical iliac blade, with no sign of the sharp lateral ridge, and a much weaker preacetabular buttress. The femoral head is similar, but it is narrower and the articular head projects further proximally in rhynchosaurs than in *Rhombopholis*.

Some of the present material could be classed as trilophosaurid. The vertebrae, however, do not correspond (cf. Gregory 1945, pls 23–25), the cervicals being shorter and higher, and the dorsals having much taller neural spines in *Trilophosaurus*, and differing considerably in detail (ADW, pers. obs. of BMNH R8302). The caudal vertebra (Gregory 1945, pl. 24) is comparable in shape, but in features common to many reptile groups. Further, only mid-tail caudals of *Trilophosaurus* are comparable to that of *Rhombopholis*, but the former have very short transverse processes (ADW, pers. obs. of BMNH R8302). The ilium of *Trilophosaurus* (Gregory 1945, pl. 28) shares a very short anterior iliac blade with *Rhombopholis*, but lacks a marked lateral ridge and preacetabular buttress. Further, the posterior process of the iliac blade seems much longer in *Trilophosaurus* than in WARMS Gz4714. The femoral head in *Trilophosaurus* (Gregory 1945, pl. 29) is massive and more equidimensional in cross section than in *Rhombopholis*. This was confirmed by direct comparison with a left femur of *Trilophosaurus* (ADW, pers. obs. of BMNH R8302). Further, the internal trochanter is not set off as such a distinctive narrow flange in *Trilophosaurus*. On balance, a case could be made that the isolated ilium and femoral head (WARMS Gz4714, Gz21) are trilophosaurid, and the vertebrae probably are not. However, the association of the proximal femur head in WARMS Gz10 with clearly non-trilophosaurid vertebrae suggests that these postcranial elements are not trilophosaurid either. The femur WARMS Gz21 is like the larger one in WARMS Gz10, although the ilium cannot be directly linked with the 'large animal' in WARMS Gz10.

The only group remaining are the prolacertiforms, a clade ranging from Late Permian (*Protorosaurus*) to Late Triassic (*Tanystropheus*). The low long cervical vertebra, the square-spined dorsals, the strong preacetabular buttress on the ilium, and the broad-headed slender femur are all shared between *Rhombopholis* and *Protorosaurus*, *Prolacerta*, *Macrocnemus*, *Malerisaurus*, and *Tanystropheus*, and the first three of these at least appear to be synapomorphies of the Prolacertiformes, or of included clades within that group. The closest resemblances of the *Rhombopholis* specimen, and the other material described here, seem to be with *Macrocnemus bassanii* (Pl. 1). In an unpublished cladistic analysis of prolacertiforms recently completed by MJB and J. A. Allen (Bristol), only five of 48 characters could be recorded for *Rhombopholis*. This was insufficient to distinguish *Rhombopholis* from other prolacertiform taxa, such as *Prolacerta*, *Macrocnemus* and *Malerisaurus*, and hence its position in the cladogram could not be determined meaningfully.

It is assumed that the reptilian bones described here represent two individuals of similar taxa, one of which is three to four times smaller than the other. None of the bones may be compared directly between the small and large animal, but both appear to be prolacertiforms. The smaller one could be a juvenile of the larger, although it lacks clear osseous indicators of juvenility: for example, the neural spines are fused to the vertebral centra, where in true juveniles a suture might still be visible.

Rhombopholis is different in size from known specimens of *Macrocnemus*. For example, femur lengths in *Macrocnemus* range from 45 to 93 mm (Peyer 1937; ADW, pers. obs.), compared with about 50 mm (preserved length of element '7' in WARMS Gz10, 44 mm) for the small English individual, and 140–150 mm for the large individual. The latter is, however, exceeded in size by species of *Tanystropheus*, with femur lengths of 48–212 mm in *T. longobardicus* (Wild 1973), and 305 mm in *T. conspicuus* (Wild 1973), and *Tanytrachelos* with femur lengths of 173–303 mm (Olsen

1979), but is similar to *Malerisaurus*, which has femur lengths of 100–120 mm (Chatterjee 1980, 1986).

Acknowledgements. This work was partly supported by NERC grant GR3/7040 and a grant from the Leverhulme Trust. We thank Simon Powell for photographic work, and Andrew Newell for Text-figure 1. We thank also Susan Evans, Nick Fraser, Glenn Storrs and David Unwin for helpful comments on the typescript, and Andrew Milner and two anonymous referees for their additional advice.

REFERENCES

ALLEN, H. A. 1909. List of British Triassic fossils in the Warwick Museum. *Report of the British Association for the Advancement of Science*, **1908 (1909)**, 274–277.

ANONYMOUS 1841*a*. The Labyrinthodon. *Salopian Journal*, **28 April 1841**, 2.

—— 1841*b*. Shropshire and North Wales Museum. *Shrewsbury Chronicle*, **30 April 1841**, 4.

BENTON, M. J. 1983*a*. Large-scale replacements in the history of life. *Nature*, **302**, 16–17.

—— 1983*b*. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London, Series B*, **302**, 605–720.

—— 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society*, **84**, 97–164.

—— 1990. The species of *Rhynchosaurus*, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. *Philosophical Transactions of the Royal Society of London, Series B*, **328**, 213–306.

—— and GOWER, D. J. in press. Richard Owen's giant Triassic frogs: archosaurs form the Middle Triassic of England. *Journal of Vertebrate Paleontology*.

—— and SPENCER, P. S. 1995. *Fossil reptiles of Great Britain*. Chapman and Hall, London, 386 pp.

—— WARRINGTON, G. R., NEWELL, A. J. and SPENCER, P. S. 1994. A review of the British Middle Triassic tetrapod faunas. 131–160. *In* FRASER, N. C. and SUES, H.-D. (eds). *In the shadow of the dinosaurs: Early Mesozoic tetrapods*. Cambridge University Press, New York, 435 pp.

CAMP, C. L. 1945. *Prolacerta* and the protorosaurian reptiles. *American Journal of Science*, **243**, 17–32, 84–101.

CARROLL, R. L. 1987. *Vertebrate paleontology and evolution*. W. H. Freeman, San Francisco, 698 pp.

CHARIG, A. J., KREBS, B., SUES, H.-D. and WESTPHAL, F. 1976. Thecodontia. *In* KUHN, O. (ed.). *Handbuch der Paläoherpetologie*, Vol. 13. Gustav Fischer, Stuttgart, 137 pp.

CHATTERJEE, S. K. 1980. *Malerisaurus*, a new eosuchian reptile from the late Triassic of India. *Philosophical Transactions of the Royal Society of London, Series B*, **291**, 163–200.

—— 1986. *Malerisaurus langstoni*, a new diapsid from the Triassic of Texas. *Journal of Vertebrate Paleontology*, **6**, 297–312.

COLBERT, E. H. 1987. The Triassic reptile *Prolacerta* in Antarctica. *American Museum Novitates*, **2882**, 1–14.

EVANS, S. E. 1988. The early history and relationships of the Diapsida. 221–260. *In* BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods. Volume 1. Amphibians, reptiles, birds*. Systematics Association Special Volume, 35A. Clarendon Press, Oxford, 377 pp.

GALTON, P. M. 1985. The poposaurid thecodontian *Teratosaurus suevicus* v. Meyer, plus referred specimens mostly based on prosauropod dinosaurs from the Middle Stubensandstein (Upper Triassic) of Nordwürttemberg. *Stuttgarter Beiträge zur Naturkunde, Serie B*, **116**, 1–29.

GAUTHIER, J. A. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences*, **8**, 1–55.

GOW, C. E. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia Africana*, **18**, 89–131.

GREGORY, J. T. 1945. Osteology and relationships of *Trilophosaurus*. *University of Texas Publication*, **4401**, 273–359.

HORWOOD, A. R. 1908. The flora and fauna of the Trias (Keuper only) in Leicestershire, with some notes on that of the surrounding counties. *Report of the British Association for the Advancement of Science*, **1907 (1908)**, 306–312.

—— 1909. Bibliographical notes on the flora and fauna of the Trias, 1826–76. *Report of the British Association for the Advancement of Science*, **1908 (1909)**, 277–282.

HOWELL, H. H. (ed.). 1859. The geology of the Warwickshire coalfield and the Permian rocks and Trias of the surrounding district. *Memoirs of the Geological Survey of the United Kingdom*, London, 57 pp.

HUENE, F. von 1908*a*. Die Dinosaurier der europäischen Triasformation mit Berücksichtigung der aussereuropäischen Vorkommnisse. *Geologische und Paläontologische Abhandlungen* (*Supplement-Band*), **1**, 1–419.

—— 1908*b*. Eine Zusammenstellung über die englische Trias und das Alter ihrer Fossilien. *Centralblatt für Mineralogie, Geologie, und Paläontologie*, **1908**, 9–17.

—— 1932. Über *Tanystropheus* und verwandte Formen. *Neues Jahrbuch für Geologie und Paläontologie, Beilage-Band, Abteilung B*, **67**, 65–86.

—— 1938. *Stenaulorhynchus*, ein Rhynchosauride der ostafrikanischer Obertrias. *Nova Acta Leopoldina, Neue Folge*, **6**, 83–121.

—— 1946. Die grossen Stämme der Tetrapoden in den geologischen Zeiten. *Biologische Zentralblatt*, **65**, 268–275.

—— 1956. *Paläontologie und Phylogenie der niederen Tetrapoden*. Gustav Fischer, Jena, 716 pp.

HULL, E. 1869. The Triassic and Permian rocks of the Midland counties of England. *Memoirs of the Geological Survey of the United Kingdom*, 1–127.

KEMP, T. S. 1982. *Mammal-like reptiles and the origin of mammals*. Academic Press, London, 363 pp.

LAURENTI, J. N. 1768. *Specimen medicum, exhibens synopsin Reptilium emendatum, cum experimentis circa venena et antidota reptilium austriacorum*. Vienna, 214 pp.

MEIGEN, J. W. 1803. Versuch einer neuen Gattungseintheilung der europäischen zweiflügligen Insekten. *Magazin für Insektenkunde*, **2**, 264.

MEYER, H. von 1847–1855. *Zur Fauna der Vorwelt. Die Saurier des Muschelkalkes mit Rücksicht auf die Saurier aus Buntem Sandstein und Keuper*. Heinrich Keller, Frankfurt-am-Main, 167 pp.

—— 1856. *Zur Fauna der Vorwelt. Saurier aus dem Kupferschiefer der Zechstein Formation*. Heinrich Keller, Frankfurt-am-Main, 28 pp.

MIALL, L. C. 1874. On the remains of Labyrinthodonta from the Keuper Sandstone of Warwick, preserved in the Warwick Museum. *Quarterly Journal of the Geological Society, London*, **30**, 417–435.

MILNER, A. R., GARDINER, B. G., FRASER, N. C. and TAYLOR, M. A. 1990. Vertebrates from the Middle Triassic Otter Sandstone Formation of Devon. *Palaeontology*, **33**, 873–892.

MORRIS, J. 1854. *A catalogue of British fossils*, 2nd edition. London, 372 pp.

MURCHISON, R. I. and STRICKLAND, H. E. 1840. On the upper formations of the New Red Sandstone System in Gloucestershire, Worcestershire, and Warwickshire; etc. *Transactions of the Geological Society, London*, (2) **5**, 331–348.

NOPCSA, F. von 1931. *Macrocnemus* nicht *Macrochemus*. *Centralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B*, **1931**, 655–656.

OERTLE, G. F. 1928. Das Vorkommen von Fischen in der Trias Württembergs. *Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie, Beilage-Band, Abteilung B*, **60**, 325–472.

OLSEN, P. E. 1979. A new aquatic eosuchian from the Newark Supergroup (Late Triassic–Early Jurassic) of North Carolina and Virginia. *Postilla*, **176**, 1–14.

ORTLAM, D. 1967. Fossile Böden als Leithorizonte für die Gliederung des Höheren Buntsandsteins im nördlichen Schwarzwald und südlichen Odenwald. *Geologische Jahrbuch*, **84**, 485–590.

OSBORN, H. F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Memoirs of the American Museum of Natural History*, **1**, 451–507.

OWEN, R. 1841*a*. [The skeleton of three species of *Labyrinthodon*]. *Athenaeum*, **1841 (718)**, 581–582.

—— 1841*b*. *Odontography; or a treatise on the comparative anatomy of the teeth*. Part ii, pp. 113–288. Hippolyte Baillière, London, 655 pp.

—— 1842*a*. Description of parts of the skeleton and teeth of five species of the genus *Labyrinthodon* (*Lab. leptognathus*, *Lab. pachygnathus*, and *Lab. ventricosus*, from the Coton-end and Cubbington Quarries of the Lower Warwick Sandstone; *Lab. Jaegeri*, from Guy's Cliff, Warwick; and *Lab. scutulatus*, from Leamington); with remarks on the probable identity of the *Cheirotherium* with this genus of extinct batrachians. *Transactions of the Geological Society, London*, (2), **6**, 515–543.

—— 1842*b*. Report on British fossil reptiles. Part II. *Report of the British Association for the Advancement of Science*, **1842 (1841)**, 60–204.

—— 1860. *Palaeontology*. A. and C. Black, Edinburgh, 420 pp.

—— 1866. *On the anatomy of vertebrates. I. Fishes and reptiles*. Longman, London, 650 pp.

PATON, R. 1974. Capitosauroid labyrinthodonts from the Trias of England. *Palaeontology*, **17**, 253–289.

PEYER, B. 1937. Die Triasfauna der Tessiner Kalkalpen. XII. *Macrocnemus bassanii* Nopcsa. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, **59**, 1–140.

PHILLIPS, J. 1871. *Geology of Oxford and the valley of the Thames*. Clarendon Press, Oxford, 529 pp.

RIEPPEL, O. 1989. The hind limb of *Macrocnemus bassanii* (Nopcsa) (Reptilia, Diapsida): development and functional anatomy. *Journal of Vertebrate Paleontology*, **9**, 373–387.

ROMER, A. S. 1966. *Vertebrate paleontology*, 3rd edition. University of Chicago Press, Chicago, 468 pp.

SCHMIDT, M. 1928. *Die Lebewelt unserer Trias*. Hohenlohe'sche Buchhandlung, Öhringen, 461 pp.

SEELEY, H. G. 1888. Researches on the structure, organisation, and classification of the fossil Reptilia. 1. On *Protorosaurus speneri* (von Meyer). *Philosophical Transactions of the Royal Society of London*, **178**, 187–213.

SHISHKIN, M. A. 1964. Suborder Stereospondyli. 83–122. *In* ORLOV, Y. A. (ed.). *Osnovy paleontologii, Vol. 5* (*Amphibia, Reptilia*). Izdatelistvo 'Nauka', Moscow, 722 pp. [In Russian].

STORRS, G. W. 1994. Fossil vertebrate faunas of the British Rhaetian (latest Triassic). *Zoological Journal of the Linnean Society*, **112**, 217–259.

TORRENS, H. S. 1992. When did the dinosaur get its name? *New Scientist*, **134**, 40–44.

WALKER, A. D. 1969. The reptile fauna of the 'Lower Keuper' Sandstone. *Geological Magazine*, **106**, 470–476.

WARRINGTON, G. R. 1976. British Triassic palaeontology. *Proceedings of the Ussher Society*, **3**, 341–353.

—— AUDLEY-CHARLES, M. G., ELLIOTT, R. E., EVANS, W. B., IVIMEY-COOK, H. C., KENT, P. E., ROBINSON, P. L., SHOTTON, F. W. and TAYLOR, F. M. 1980. A correlation of Triassic rocks in the British Isles. *Special Report of the Geological Society of London*, **13**, 1–78.

WILD, R. 1973. Die Triasfauna der Tessiner Kalkalpen. XXIII. *Tanystropheus longobardicus* (Bassani) (Neue Ergebnisse). *Schweizerische Paläontologische Abhandlungen*, **95**, 1–162.

WILLS, L. J. 1910. On the fossiliferous Lower Keuper rocks of Worcestershire. *Proceedings of the Geologists' Association*, **21**, 249–331.

WOODWARD, A. S. and SHERBORN, C. D. 1890. *British fossil Vertebrata*. Dulau, London, 390 pp.

MICHAEL J. BENTON

Department of Geology
University of Bristol
Bristol BS8 1RJ, UK

ALICK D. WALKER

17 Kingsley Avenue, Melton Park
Newcastle-upon-Tyne NE3 5QN, UK

Typescript received 12 July 1995
Revised typescript received 9 November 1995